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THE INFLUENCE OF SEED DISPERSAL AND PREDATION ON FOREST ENCROACHMENT INTO A CALIFORNIA GRASSLAND

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ABSTRACT

Forest encroachment into grasslands is a widespread phenomenon with significant implications for land management. We examined the influence of seed dispersal and predation on the encroachment of two tree species, *Lithocarpus densiflora* and *Pseudotsuga menziesii*, into a coastal California grassland. We mapped the distributions of *L. densiflora* and *P. menziesii* seedlings and saplings and *L. densiflora* acorns across the forest-grassland ecotone as well as quantified the fates of seeds of both species experimentally located at five distances across the ecotone. Species distributions varied, with *P. menziesii* being most abundant in the grassland and at the edge and *L. densiflora* in the forest. *Lithocarpus densiflora* acorns were absent from the grassland but equally abundant at the edge and forest. Seed predation was similar for both species, being low in the grassland, variable at the edge, and high in the forest. It appears that *L. densiflora* encroachment into the grassland is strongly influenced by seed dispersal, while *P. menziesii* encroachment is more likely influenced by seed predation than dispersal.

Key Words: forest-grassland ecotone, seed dispersal, seed predation, woody plant establishment, *Pseudotsuga menziesii, Lithocarpus densiflora.*

Woody plant-grassland ecotones have been postulated to remain stable for long ecological time periods (Griffin 1977; Davis and Mooney 1985); however, many studies have documented an increase in woody plant encroachment into grasslands in recent years (Van Vetgen 1983; Hobbs and Mooney 1986; Archer 1989; Trollope et al. 1989; Roques et al. 2001). A number of mechanisms have been proposed to explain the increase in encroachment including climate change (Polley et al. 1997), fire suppression (Bragg and Hurlbert 1976; Callaway and Davis 1993), succession (Archer 1988), and over-grazing (Archer 1995; Roques et al. 2001). While each of these factors can be important and they are not mutually exclusive, the specific determinants of woody plant encroachment often vary among environments (Scholes and Archer 1997).

In coastal California, fire was a primary historical factor controlling the stability of woody plant-grassland ecotones (Griffin 1977; Greenlee and Langenheim 1990; Keeley 2002). The high frequency of Native American burns and fires caused by lightning maintained a mosaic of grasslands, shrublands, and forests throughout the coastal region (Keeley 2002). Over the past two centuries, however, policies of fire suppression have effectively reduced fire frequency (Minnich 1983; Greenlee and Langenheim 1990), and this suppression has corresponded with the increase of woody plant encroachment into grasslands (McBride and Heady 1968; McBride 1974; Callaway and Davis 1993; Keeley 2002).

Although the absence of fire appears to be a key factor allowing for woody plant establishment in grasslands, a suite of other ecological factors can also influence encroachment dynamics (Scholes and Archer 1997). Much of the research in California has focused on the changes in light and soil moisture among grasslands and woody plant communities (Davis and Mooney 1985; Hobbs and Mooney 1986; Williams and Hobbs 1989; Muick 1991), the competitive interactions among woody plants and grasses (Griffin 1971; Gordon et al. 1989; Danielson and Halvorson 1991), and the effects of animal herbivory (Griffin 1980; Davis et al. 1991). In addition to these factors, other research outside California suggests that both seed dispersal and predation may also be important in controlling woody plant encroachment (Stapanian and Smith 1986; Brown and Archer 1987; Kollman and Schill 1996; Hubbard and McPherson 1999). While the relative significance of these different ecological factors is likely to vary among locations, factors affecting encroachment have also been shown to have hierarchical and interactive effects (House et al. 2003). Because seed dynamics can have a major influence of seedling distributions and abundances, analyzing this life stage in conjunction with later stages may be particularly important in understanding patterns of woody plant encroachment.

At our research site on Mount Tamalpais, California, where both fire and grazing have been excluded from the grasslands for the past 50 years (M. Swezy personal communication), there has been widespread woody plant encroachment (Fig. 1). The objective of this paper was to examine the influence of seed dispersal and predation on the en-

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FIG. 1. Forest encroachment in the grasslands along Bolinas ridge, Mt. Tamalpais, CA (37°54′N, 122°37′W).

croachment of the dominant forest tree species, *Lithocarpus densiflora* (Hook. & Arn.) Rehder and *Pseudotsuga menziesii* (Mirbel) Franco, into the grassland. To quantify the rates of encroachment, we mapped the locations of *L. densiflora* and *P. menziesii* seedlings and saplings at five distances across the forest-grassland ecotone. We also quantified the natural acorn rain of *L. densiflora* at those distances and the movement of acorns placed at the forest edge. Finally, we experimentally manipulated the locations of *P. menziesii* seeds and *L. densiflora* acorns across the forest-grassland ecotone and followed their fate over five week periods.

METHODS

Study Area and Species

The study was conducted along Bolinas ridge in the Marin Municipal Water District watershed on Mount Tamalpais (37°54′N, 122°37′W) in southern Marin County, CA. The 9000-ha watershed encompasses a mix of vegetation types, including grassland, chaparral, and mixed evergreen forest (Parker 1991). The mixed evergreen forest is dominated by *P. menziesii* (hereafter referred to as *Pseudotsuga*) and *L. densiflora* (hereafter referred to as *Lithocarpus*), with *Quercus agrifolia* Nee, *Quercus chrysolepis* Liebm., *Arbutus menziesii* Pursh, *Umbellularia californica* (Hook. & Arn.) Nut., and *Sequoia sempervirens* (D. Don) Endl. also present (Horton et al. 1999). The grasslands are a mixture of exotic annuals and native and exotic perennials dominated by *Danthonia californica* Boland, *Bromus carinatus* (Nutt. ex Buckl.) Shear, *Lolium multiflorum* Lam., and *Briza major* K.Presl (J. Corbin personal communication). The study area is characterized by a mediterranean climate with a seasonal summer dry period and average annual precipitation of 1250 mm (Dunne and Parker 1999). Soils in the grassland are classified as composites of the Saurin clay loam and Bonnydoon gravelly loam series and in the forest, Centissima loam-Barnabe very gravelly loam series (U.S.D.A. 1990).

The two tree species disperse their seeds between August and December. *Lithocarpus* acorns can fall as early as late August, but early acorns are generally immature and insect infested (P. Kennedy personal observation). Mature acorns typically fall between late September and late November (Tappeiner et al. 1990). *Pseudotsuga* seeds fall rapidly after the cones mature and approximately two-thirds of the total seed crop is on the ground by late October (Hermann and Lavender 1990).

Seed size and dispersal method vary between species. *Lithocarpus* acorns range from 2–5 cm long × 1–2 cm wide and are primarily small-mammal and bird dispersed (Tappeiner et al. 1990). The western grey squirrel (*Sciurus griseus*) is the primary disperser in the study area, although the Steller's jay (*Cyanocitta stelleri*) may also move acorns (P. Kennedy personal observation). Primary acorn predators include the aforementioned dispersers, the acorn woodpecker (*Melanerpes formicivorus*), and potentially the California mouse (*Peromyscus californicus*; see Kalcounis-Ruppell and Millar 2002 about *P. californicus*). Insects such as filbert weevils (*Curculio occidentalis*) are also important acorn predators (Lewis 1991); however, their effects were not addressed in this study. *Pseudotsuga* seeds are 6–12 mm long × 2–4 mm wide and primarily wind-dispersed (Hermann and Lavender 1990). The seeds are consumed by a wide range of insect, small mammal, and bird species (Gashwiler

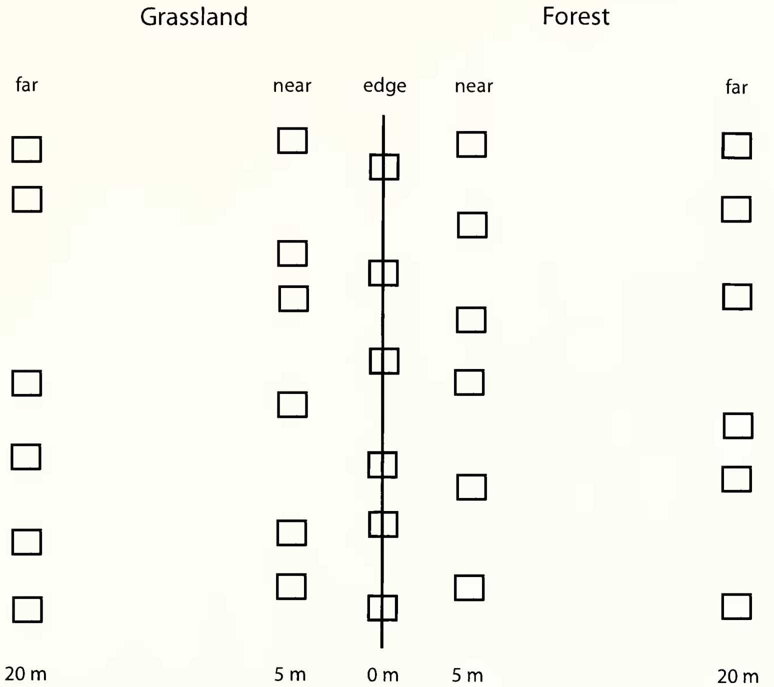

FIG. 2. Sampling design across the forest-grassland ecotone. The squares represent one m^2 plots randomly located at each distance. See text for details of plot replication.

1968). Due to differences in dispersal mode, we hypothesized that *P. menziesii* would have higher seed and therefore seedling and sapling densities in the grasslands than *L. densiflora*. Additionally, we hypothesized that the intensity of seed predation would be lower in the grasslands for both species because there is less vegetative cover to protect seed dispersers from predators.

Sampling and Experimental Design

Seedling and sapling distributions. In February 2003, we haphazardly selected five sites with evidence of woody plant encroachment. The sites were located 0.2–1 km apart. At each site, five distances across the forest-grassland ecotone were located: far grassland (20 m into the grassland), near grassland (5 m into the grassland), edge (at the forest-grassland ecotone edge), near forest (5 m into the forest), and far forest (20 m into the forest). The forest-grassland edge was defined as the location where the branches of forest trees were present at 2 m above the ground. In all cases, the edge was very easy to delineate given the large differences in age between trees in the forest and those in the grassland. At each distance, six 1-m^2 plots were randomly established along a 20-m transect running parallel to the ecotone edge (Fig. 2). Within each plot, all *Lithocarpus* and *Pseudotsuga* individuals less than ten cm diameter at breast height (DBH) were counted. Individuals were divided into two age classes: those with a DBH between one and ten cm were considered saplings and those with a DBH less than one cm or without a DBH were considered seedlings. We first calculated the proportion of plots in which each species was present at each distance and site. Using site as the level of replication, we then conducted a two-way (species and distance) fixed factor analysis of variance (ANOVA) to analyze distributions across the ecotone ($n = 25$ plots per species). The variances were first determined to be homogenous using Cochran's C test ($P > 0.05$).

Acorn distributions. To sample *Lithocarpus* acorn distributions across the ecotone, we randomly selected different five sites that had at least one acorn-producing *Lithocarpus* individual in the forest canopy within 20 m of the ecotone edge. The sites were located 0.3–1.5 km apart. Using the identical sampling design as above, we counted the number of whole fallen 2002 acorns within each 1-m^2 plot on 1 November 2002 (distinguished from older acorns by color and surface texture). We used a two-way mixed model ANOVA, with site (random) and distance (fixed) as the model factors to analyze the acorn distributions ($n = 150$ plots). The data were first $\log(X + 1)$ transformed to make variances homogenous (Cochran's C test). Tukey HSD tests were used for *a posteriori* comparisons between means within each site.

Seed dispersal and handling experiment. In early October 2002, *Lithocarpus* acorns were collected along Bolinas ridge. In the laboratory, acorns were immersed in water and all those floating after five minutes were considerable inviable (Nyandia and McPherson 1992). Viable acorns were surface sterilized in a 10% bleach solution for five minutes, air dried, and stored at 4°C for a week before tagging. All *Pseudotsuga* seeds were collected from a nearby coastal forest and provided by the U.S. Forest Service, Placerville nursery.

The acorn tagging method was modified from Forget et al. (1998). A 1-mm diameter hole was drilled through the center of the acorns and threaded with a 1-m piece of clear fishing line. The line was knotted on both sides of the acorn, and a small numbered tag was attached to the opposite end. *Pseudotsuga* seeds were not tagged due to their small size. Instead, they were individually placed on outer edge of 5 × 2.5 cm sticky whitefly cards (Safer Inc., Bloomington, MN) when put in the plots. The sticky cards were necessary because the *Pseudotsuga* seeds could not be relocated in the grasslands or forest floor without them. Although the sticky cards may have potentially altered the behavior of seed predators, all seeds were placed on sticky cards; therefore, their effect should be similar at all distances.

In mid-October 2002, two sites, separated by 1 km, were randomly selected. At both sites, the same far grassland, near grassland, edge, near forest, and far forest distances as above were located (Fig. 2). At each distance, a 50-m transect running parallel to the forest-grassland ecotone was delineated. Along each transect, 15 one-m^2 plots separated by least one m were established. The plots were randomly assigned as follows: six plots with tagged *Lithocarpus* acorns, three plots with untagged *Lithocarpus* acorns, and six plots for *Pseudotsuga* seeds ($n = 90$ *Lithocarpus* plots and $n = 60$ *Pseudotsuga* plots). Within the acorn plots, eight acorns were randomly located on the soil surface ($n = 720$ acorns total). In the *Pseudotsuga* plots, four seeds (each on an individual sticky card) were put on the soil surface at the four corners of the plot ($n = 240$ seeds total).

Lithocarpus acorns were put out from October 15–November 15 and *Pseudotsuga* seeds November 10–December 10. Each acorn and seed was scored as "handled" or not. Handling was defined as eaten, buried, moved, or disappeared. Although some of the buried, moved, or missing acorns may have escaped predation, the number of moved and missing acorns was low, and many studies have shown that the majority of buried acorns are eventually eaten (see Van der Wall 2001). Therefore, we consider handling to be a maximum estimate of predation. We could not determine the fate of untagged but handled acorns or *Pseudotsuga* seeds and therefore scored these only as handled or not. Seed handling was calculated as the proportion of seeds handled in each plot.

Pooling the tagged and untagged acorn data (a prior analysis showed no significant effect of tagging), we analyzed acorn handling using a two-way mixed model ANOVA, with site (random) and distance (fixed) as the model factors. Although the variances were still heterogeneous after an arcsine transformation (Cochran's C test, $P < 0.05$), ANOVAs are robust to departures from variance assumptions in large experiments where the data are balanced (Underwood 1997). Tukey HSD tests were used for *a posteriori* comparisons between means. *Pseudotsuga* seed handling was analyzed with a two-way mixed model ANOVA, with site (random) and distance (fixed) as the model factors. Variances were determined to be homogenous (Cochran's C test, $P > 0.05$), and Tukey HSD tests were used for *a posteriori* comparisons between means.

RESULTS

The distributions of the *Lithocarpus* and *Pseudotsuga* differed considerably across the ecotone (significant species × distance interaction: $F_{4,40} = 18.123$, $P < 0.001$) (Fig. 3). *Lithocarpus* occurrence was much higher in forest than at the edge or grassland. Conversely, *Pseudotsuga* had much higher occurrence in the grassland and edge than in the forest. Eighty-two and 96% of *Pseudotsuga* seedlings and saplings, respectively, were located at the edge or in the grassland, whereas 80% and 91% of the *Lithocarpus* seedlings and saplings, respectively, were located in the forest.

Lithocarpus acorn densities varied significantly by distance ($F_{4,125} = 6.710$, $P = 0.002$), with no acorns ever found in the far or grassland plots and variable densities among the edge, near forest, and far forest distances across sites (Fig. 4). Acorn densities varied also across the five sites ($F_{4,125} = 3.446$, $P = 0.010$), most likely due to the variation in the number of acorn producing *Lithocarpus* individuals at each site. Because the number of acorns at the edge, near forest, and far forest differed between sites there was also a significant site and distance interaction ($F_{16,125} = 4.299$, $P < 0.001$).

The handling of both *Lithocarpus* acorns and *Pseudotsuga* seeds differed significantly among distances (*Lithocarpus*: $F_{4,80} = 295.030$, $P < 0.001$; *Pseudotsuga*: $F_{4,50} = 35.00$, $P = 0.002$), but not between sites (*Lithocarpus*: $F_{1,80} = 0.765$, $P = 0.384$; *Pseudotsuga*: $F_{1,50} = 0.745$, $P = 0.392$). *Lithocarpus* handling was low at both grassland distances, medium at the edge, and high at both forest distances (Fig. 5). Of all the acorns handled, 59% were eaten, 26% buried, 12% moved, and 3% disappeared. *Pseudotsuga* showed the same general pattern of seed handling, although the edge and far forest were not significantly different, and the near forest had significantly higher handling than all other distances (Tukey HSD tests, $P < 0.05$). There were no significant higher-order interactions for either species.

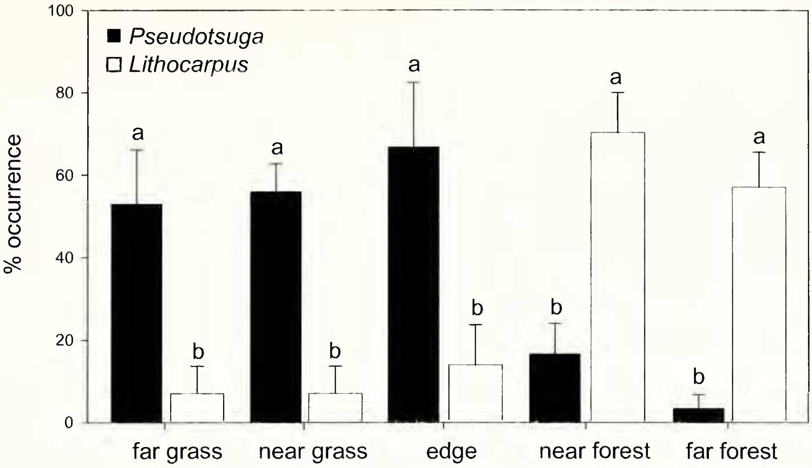

FIG. 3. Mean percent occurrence ± one standard error of *Lithocarpus* (light bars) and *Pseudotsuga* (dark bars) seedlings and saplings (combined) across the forest-grassland ecotone from five sites. Different letters indicate significant differences (Tukey HSD tests, $P < 0.05$).

DISCUSSION

Based on both the acorn distributions and seed handling experiment, it appears that dispersal limitation is the major factor inhibiting the *Lithocarpus* encroachment. Although we did not directly measure the dispersal of *Pseudotsuga* seeds in this study, there is an abundance of theoretical and empirical research that demonstrate that *Pseudotsuga* seeds are often dispersed over distances greater than *Lithocarpus* (Hermann and Lavender 1990). Most studies of *Pseudotsuga* seed dispersal show declining abundance moving away from forest edges; however, densities can remain relatively high in areas close to forests (see Mair 1973 and citations within). Gashwiler (1969) found that seed abundance was approximately 60% that in the intact forest at 30 m from the forest edge and McDonald (1980) documented an average of 4257 sound seeds/ha up to 60 m from the forest edge. These studies suggest that *Pseudotsuga* seed dispersal into the grassland is quite high, particularly at shorter distances. These dispersal results are also consistent with those predicted by Clark et al. (1999), who modeled the seed dispersal of a number of temperate and tropical tree species and showed that wind-dispersed species were consistently dispersed farther than animal-dispersed species. Compared to the animal-dispersed seed shadows, many wind-dispersed conifer species still had considerable seed shadows at distances ≥40 m.

The absence of *Lithocarpus* acorns in the grassland is most likely due to very limited dispersal by small mammals and birds. While some studies demonstrate that animals do transport acorns into grasslands (Darley-Hill and Johnson 1981; Stapanian and Smith 1986; Kollman and Schill 1996), others have shown that dispersers, particularly small mammals, may not frequent areas with less vertical plant cover (Kikuzawa 1988; Miyaki and Kikuzawa 1988; Quintana-Ascencio et al. 1992; Wada 1993). These movement patterns may different abundances of predators in different habitats (Brown et al. 1999) or simply that animals that spend most of their time in the forest are more likely to eat or disperse food items in the areas where they spend the majority of their time. Despite the fact seed dispersal into the grasslands appeared to be very limited, the seedling and sapling distributions confirm that occasionally *Lithocarpus* acorns are dispersed into the grassland and get established. Therefore, over longer ecological time periods, *Lithocarpus* may show significant encroachment. The lack of correspondence that we observed between the acorn and seedling distributions in the grassland may also be related to the fact that birds remove many acorns before they ever hit the ground (Koenig and Knops 1994). This could have caused us to either over- or underestimate the amount of dispersal into grasslands depending on number of birds that were dispersers versus predators at our sites.

Our results from the seed handling experiment are consistent with those of other studies of acorn predation along forest-grassland ecotones. Stapanian and Smith (1986) found that squirrels cached *Quercus* spp. acorns and *Juglans nigra* L. nuts more often if they were closer to forest edges than in the prairies. In fact, they found that no acorns beyond nine meters into the prairies were ever handled. Hubbard and McPherson (1999) also found lower rates of seed predation in grasslands than adjacent oak woodlands, but handling did occur up to 50 m into the grasslands. In our study, a very small proportion of acorns in the near grassland (5 m) and far grassland (20 m) plots were handled and the handling that did occur may have been caused

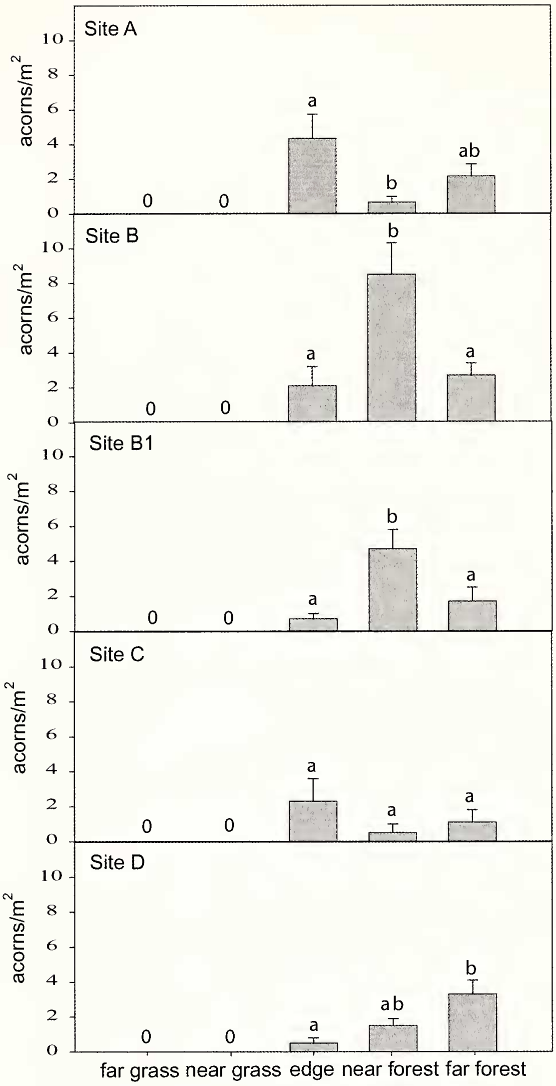

FIG. 4. Mean *Lithocarpus* acorn densities (one standard error) across the forest-grassland ecotone at five sites. Different letters indicate significant differences within each site (Tukey HSD tests, $P < 0.05$).

by gopher activity rather than small mammal predation (the plots with acorns removed had fresh gopher mounds) (Borchert et al. 1989). We are not aware of any other studies that examine *Pseudotsuga* seed handling across a natural forest-grassland ecotone, but Gashwiler (1968) documented that *Pseudotsuga* seed predation in clear-cuts could be quite high. However, Nystrand and Granstrom (2000) found that *Pinus sylvestris* L. seed predation was higher in intact forests than clear-cuts. We believe the effects of *Pseudotsuga* seed handling across the ecotone may be mediated by spatial variation in seed quantity. Although a greater proportion of fallen seeds were handled at the edge than in the grassland, there are likely to be more seeds present at the edge due to closer proximity to adult trees. As a result, the number of seeds escaping predation in these two habitats may be equivalent, which may explain the equal occurrence of *Pseudotsuga* seedlings and saplings across these distances. In the forest, however, where predation is much higher than at the edge or grassland, seed predators may consume the majority of seeds regardless of the increased seed quantity.

Although seed dispersal and predation may play a significant role in forest encroachment, changing environmental conditions across the forest-grassland ecotone may also affect patterns of establishment. Generally, *Pseudotsuga* establishment and growth is much higher in less shaded environments (Herman and Lavender 1990; Harrington and Tappeiner 1997; Hunter 1997). Because of the low light levels in the forest, its lower seedling and sapling abundances in that habitat may have been driven more by light than seed predation. In contrast, *Lithocarpus* establishment and growth appears to be less sensitive to low light (Harrington and Tappeiner 1997; Hunter 1997). In fact, many oak seedlings actually show better recruitment in shaded than open areas. For example, Callaway (1992) found that the survival of *Quercus douglasii* Hook. & Arn, but not *Q. lobata* Nee, was significantly higher under a shrub canopy than in open grasslands in coastal California. Cruzan (1981) reported the same pattern of increased survival in shaded versus unshaded grassland plots with *Q. agrifolia* and Williams et al. (1991) with *Q. durata* Jepson. In addition to light effects, soil moisture also changes considerably across the forest-grassland ecotone and can be very low in the grassland during the summer months (P. Kennedy unpublished data). Dunne and Parker (1999) documented that first-year *Pseudotsuga* seedling survival in California chaparral, where summer soil moisture consistently dropped to −8.0 MPa, was very low. Little is known about the effects of water stress on *Lithocarpus,* but Harrington et al. (1994) indicated that *Lithocarpus* saplings may be more water stress tolerant than *Pseudotsuga.* Given the importance of these environmental factors in tree seedling establishment and growth, we emphasize the likely potential for forest encroachment to be driven by a series of hierarchical and interactive factors that should not be considered in isolation (House et al. 2003). In addition to this study, we are currently investigating a number of other abiotic and biotic factors affecting forest encroachment on Mount Tamalpais, which will allow us to better determine the specific importance of seed dispersal and predation relative to other factors such as light, soil moisture, herbivory, and mycorrhizal fungi.

In summary, we found that seed dispersal and predation may influence forest encroachment in grasslands, although their effects vary between species. While *Lithocarpus* encroachment into the grassland appeared to be strongly dispersal limited,

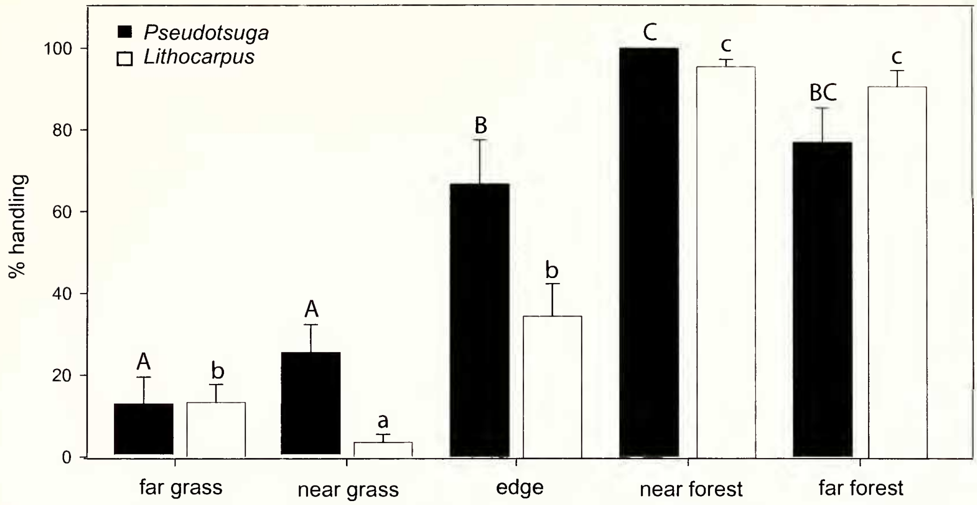

FIG. 5. The mean percent handling ± one standard error of *Lithocarpus* acorns and *Pseudotsuga* seeds across the forest-grassland ecotone from two sites. See text for definitions of handling. Different letters indicate significant differences (Tukey HSD tests, $P < 0.05$); lower-case letters for *Lithocarpus* and capital letters are for *Pseudotsuga.*

Pseudotsuga encroachment is more likely to be influenced by seed predation than dispersal. Seedling and sapling distributions indicate that *Pseudotsuga* is encroaching into the grassland much more rapidly than *Lithocarpus,* which is most likely due to higher seed dispersal into the grassland combined with relatively low seed predation. However, due to the short-term nature and specific focus of this study, future studies incorporating longer time scales and other factors will better integrate the relative importance of seed dispersal and predation into forest-grassland shifts through time. Specifically, further studies of the ecological factors affecting the survival and growth of subsequent plant life stages of these species are needed to more fully understand the dynamics of forest encroachment in this system.

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